VOLUME XXV NUMBER 2

# BOTANICAL GAZETTE

*FEBRUARY 1898*

## CONTRIBUTION TO THE LIFE-HISTORY OF RANUNCULUS.[1]

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(WITH PLATES IV–VII)

IN 1896 a group of research students working in the Hull Botanical Laboratory of the University of Chicago began the investigation of a somewhat wide range of spermatophytes. In addition to the individual problems certain representative forms were selected for joint study, among which was Ranunculus. It was felt that a large multiplication of preparations was desirable, in at least a few cases, to discover the possibilities in variation, and this feeling was justified by the result, since very different conclusions could be drawn from different sets of preparations. It is comparatively easy to obtain a definite sequence in the development of structures when the facts are few, but definite sequences seem to disappear as facts multiply.

The species of Ranunculus chiefly studied were *R. septentrionalis*, *R. multifidus*, and *R. abortivus*, and the results obtained were so constant that it would not be profitable to distinguish in every case among the species in the following account. Certain other genera of Ranunculaceæ were examined also, and they contribute to certain conclusions herein set forth.

[1] Contributions from the Hull Botanical Laboratory. VII. The previous contributions will be found in BOT. GAZ. **20**: 205–212. 1895; **23**: 40–43, 147–179, 252–273, 412–452. 1897; **24**: 93–102. 1897.

It is hardly necessary to refer to the history or literature of this subject, as it has been presented frequently. The paper simply presents certain results obtained from Ranunculus, in reference to structures with whose "normal" behavior morphologists are entirely familiar. It was felt that Ranunculus might be of interest from a phylogenetic point of view, as representing one of the so-called "primitive regions" of dicotyledons.

The usual methods of killing, staining, and sectioning were used, and need no special description.

## MICROSPORANGIA AND MICROSPORES.

In the young sporangium a plate of hypodermal cells becomes distinctly differentiated by means of their enlarging radial diameter and prominent nuclei (*fig. 1*). There is great confusion in terminology in reference to these cells and those derived from them, and it is in the interest of clear statement to establish homologous parts, so far as possible, and adopt a uniform terminology. In case this is not possible, at least a consistent terminology should be used throughout a single paper or text. Deferring a brief discussion of this matter to the end of the section, I would regard this plate of cells as the archesporium. Each archesporial cell tends to develop a radial row, and this arrangement remains more or less distinct in spite of certain inequalities of development in neighboring cells. Tracing the development of a single archesporial cell, the sequence of events is very similar to that commonly found in connection with the archesporial cell of the macrosporangium. A periclinal division results in two cells radially placed (*fig. 1*), the outer of which is a primary wall cell and the inner a primary sporogenous cell. From this point, the sequence is variable. Both cells may divide by periclinal walls, or the primary sporogenous cell may divide only in the formation of mother cells. In the former case, the outer cell formed by the periclinal division of the sporogenous cell contributes to the formation of the tapetum. In the latter case the innermost cell derived from the two or three periclinal divisions of the primary wall cell contributes to the tapetum (*figs. 2, 3*).

It would appear that in Ranunculus the cells of the peripheral region of the tapetum may be variable in origin. Of course the tapetal cells on the axial side of the sporogenous tissue cannot in any event be derived from the primary wall cells. The tapetum, therefore, is essentially a morphological composite, and is significant only in its physiological relation to the sporogenous cells. In its peripheral region in Ranunculus it may be derived from the primary wall cell, as in the eusporangiate Filicineæ; or from the primary sporogenous cell, as in the leptosporangiate Filicineæ. In its axial region it may be derived from the adjacent tissue, or cut off from the sporogenous tissue. In some cases it seemed as though the whole of the tapetum were cut off from the periphery of the sporogenous tissue (*fig. 4*), and in other cases (*fig. 5*) its partial derivation at least from primary wall cells seemed equally clear. In the case of an archesporium consisting of a single longitudinal row of cells, as in Cnicus, it was observed that all the cells of the tapetum, with the possible exception of a single peripheral one, were derived from the adjacent tissue. While there may be uniformity in the origin of the tapetum in some cases, enough was seen of the history of the individual archesporial cells to indicate that the cell of the radial row contributing to the tapetum might be sister to the contiguous sporogenous cell, or to a cell derived from the primary wall cell. In any event, the main fact seems to be that each archesporial cell develops a radial row with a varying number of cells; that the innermost cell of this row is sporogenous; that the outer ones are sterile; and that between the two a special nutritive layer is developed (the tapetum) whose constituent cells are determined by position rather then by origin. In general there are two layers of cells in the wall of the sporangium between the endothecium and the tapetum (*fig. 6*), but the number may vary between one and three in the same wall. The cells of the tapetum are occasionally binucleate (*fig. 4*), but not mostly so, as in many other microsporangia examined. In *Hepatica acutiloba* tapetal cells were observed containing from six to thirteen nuclei.

The primary sporogenous cells do not divide extensively, each cell dividing once or twice, so that the mother cells are only two or three times as numerous as the primary sporogenous cells (*fig. 6*). Disorganization of the tapetum and wall layers begins early, so that the mother cells soon become quite free in the loculus (*figs. 4, 6*).

In the development of microspores the usual sequence of events was observed, an ordinary series being shown in *figs. 7-10*. The four spores may be arranged in the usual tetrahedral fashion (*fig. 11*), or may lie in the same plane (*fig. 12*). In both divisions of the mother cell numerous free nucleoli were observed in the cytoplasm (*figs. 12, 13*), and in some cases the bodies were noted which have been regarded as centrosomes (*fig. 14*). In the mature spore the exospore develops fifteen to thirty thin spots for tube extrusion (*fig. 15*).

In the germination of the spore but a single nuclear division was observed in the spore itself, the tube and generative nuclei being approximately of equal size and form (*figs. 16, 17*). In the figures cited it will be noted that the organization of the two into distinct cells has not been accomplished. In Caltha the same division was observed, and upon the complete organization of the generative cell it assumed the usual lenticular form. This form may involve the nucleus itself, or it may be due entirely to the aggregation of the cytoplasm in polar position, the whole distinctly invested by a "Hautschicht."

The term archesporium must either be restricted so as to apply only to those cells which produce mother cells or their equivalents, or it must be extended so as to include those differentiated cells which produce wall cells, tapetum, and sporogenous cells. It is in the latter sense that the term has been used above. This has seemed the more desirable use of the term, as it is far more definite and easy of application. Such a cell is distinctly differentiated, but its progeny may vary considerably, and in the case of Ranunculus the restricted use of archesporium might or might not involve the tapetum.

In the first division of an archesporial cell, in its larger

application, the exterior cell has been called the "primary wall cell," as its derivatives enter into the formation of the wall; rather than the "primary tapetal cell," as its derivatives may or may not contribute to the tapetum. The interior cell resulting from the first division of an archesporial cell is well called a "primary sporogenous cell," as the sporogenous tissue is derived from it, and often nothing else is.

This very customary use of the term archesporium in connection with the microsporangia of spermatophytes, when logically applied to the macrosporangia of spermatophytes and the sporangia of other groups, leads sometimes to a terminology not at all customary. In the case of the macrosporangia of spermatophytes the term archesporium is applied in the same broad sense to the first distinctly differentiated cell. In this cell a periclinal division may or may not take place. If it does occur, as is usual, the exterior sterile cell has been called a tapetal cell, whether it functions as a tapetum or not, and whether it divides further or not. It seems evident that we have here the homologue of the primary wall cell of the microsporangia, which may form several layers, to call all of which a tapetum seems very questionable. In this case it is a question whether the problematical so-called "potential macrospores" do not function as tapetal cells, in which case the "fertile macrospore" may be regarded as the only real sporogenous cell. In view of the uncertain nature of these structures, however, no such terminology is adopted, and the current view that they are spore mother cells is retained.

In such sporangia as those of the eusporangiate Filicineæ, however, a similar application of the term archesporium changes its usual application. The distinctly differentiated superficial cell becomes in this case the archesporium, and the usual periclinal division separates the exterior primary wall cell from the interior primary sporogenous cell (not archesporium).

In the case of such extremely modified sporangia as those of the leptosporangiates, the archesporial cell functions as an apical cell in the development of the stalk, but the usual peri-

clinal division finally separates an exterior primary wall cell from an interior primary sporogenous cell. In this latter case the tapetal layer is evidently cut off from the sporogenous cell, but we have seen that this may occur in other groups as well.

Such an application of the term archesporium has the merit of uniformity and of fairly homologizing its derivatives. It has seemed to me that the term tapetum should disappear as a morphological term, inasmuch as it is a physiological layer between the sporogenous cells within and the sterile cells without, and of variable origin, derived from the wall cells, or from the sporogenous cells, or from the cells of the adjacent tissue.

## MACROSPORANGIA AND MACROSPORES.

In the case of *R. septentrionalis* a single hypodermal cell frequently represents the whole of the archesporium (*figs. 18–22*), soon becoming very much larger than the contiguous cells, and with a very conspicuous nucleus. Frequently an axial row of cells beneath this archesporial cell, with prominent nuclei, gives the impression of a row of mother cells (*figs. 19, 21*), but the subsequent history of the larger hypodermal cell proves the contrary. In most cases the epidermal cells capping the single archesporial cell divide once by a periclinal division (*figs. 20, 23*), or occasionally twice, making three layers of cells, but this represents all the development of tissue above the sporogenous cells. In this case no primary wall cell (tapetum) is derived from the archesporium.

In many cases, however, instead of a single archesporial cell, a group of cells forms the archesporium. Regarding only those cells which show by their increased size, prominent nuclei, and reaction, that they are of undoubted archesporial nature, numbers varying from two to thirteen were observed (*figs. 24–26*). In *fig. 26* an archesporium of eight cells is shown. In many cases it was hard to define the archesporium exactly, as cells contiguous to those of undoubted archesporial nature, by virtue of their size and general appearance, certainly suggested archesporial character. The evidence is clear that the single arche-

sporial cell of Ranunculus is but the remnant of an archesporial mass of cells, which still appears in various stages of sterilization. In some cases two or three cells of a several-celled archesporium were observed to develop to mature size, but usually not more than one was observed to divide. In certain preparations, however, development of several of the archesporial cells was observed to have proceeded further (*fig. 27*), some developing to the "two-celled" and "four-celled" condition of the embryo sac. In the case of *R. septentrionalis*, on account of imperfect material, only a single stage of development was noted, but as a complete series was obtained from *R. multifidus*, it seems probable that the same division into four mother cells occurs. In no case was a primary wall cell (tapetal cell) cut off, the archesporial cell dividing directly into mother cells.

In *R. multifidus* the sequence of events from archesporium to macrospore was obtained in detail. Indication of an occasional two or three-celled archesporium was also observed (*fig. 28*). The series of changes from the archesporial cell to the axial row of four mother cells is represented in *figs. 29–32*, and in every case observed the lowest cell of the series developed the macrospore.

In *R. abortivus* the same stages were observed. *Fig. 33* represents a notably well-developed archesporium of two cells, while *figs. 34* and *35* indicate the same steps in the development of the macrospore as those observed in *R. multifidus*. In the last two figures the condition of the integuments indicates the stage of the ovule in which the sporogenous development occurs.

In its earliest condition, after distinct differentiation, the macrospore of *R. septentrionalis* is almost globular (*fig. 36*), with prominent nucleus and nucleolus. Soon it begins to elongate in the direction of the long axis of the nucellus, with enlargement of the nucleus and characteristic ante-division nuclear changes (*fig. 37*). In some cases the macrospore becomes so much elongated as to be cylindrical. The series of nuclear divisions which occur in the macrospore is indicated in *figs.*

*38–42*, in which may be noted also the constant development of a large vacuole separating the micropylar and antipodal nuclei. The preparations of *R. multifidus* were much more favorable for a study of the mature condition of the embryo sac than those of *R. septentrionalis*. The series shown in *figs. 43–47* may be taken as fairly representative of the mature sac in *R. multifidus*. The strong development of the antipodal cells is a notable feature, distinct walls being developed, the cells enlarging in size and giving evidence of great activity until late in the endosperm formation. The formation of the very large definitive nucleus is plainly shown, and its placing near the oosphere. The general insignificance of the nuclei of the egg apparatus as compared with the others, and their relatively late organization into cells, is at once remarked, synergid nuclei being especially small. In *figs. 43–46* the fact that the synergids are sister cells is evident, and the shifting position of the micropylar nuclei can be traced.

The prominence and activity of the antipodal cells is more marked in certain other ranunculaceous plants than in Ranunculus itself. *Thalictrum purpurascens* and *Hepatica acutiloba* (*fig. 48*), can be taken as illustrations. Associated with the growth of these cells is the usual abundant nuclear division, which, although in every case apparently mitotic, is more or less irregular, as indicated in *figs. 49, 50*, both of which represent the antipodal cells of Hepatica.

It has long since become evident that the most variable region of the embryo sac in dicotyls, preceding fertilization, is the antipodal region. The old formula of three dwindling and evanescent cells, with or without walls, is far from adequate. Such a statement seems to be more true of monocotyls than of dicotyls. In the latter I am able to distinguish at least four distinct types of antipodal development, with the vast majority of forms yet to be investigated. These types merge into one another, but are distinct enough in their extreme expression.

1. A group of evanescent cells, usually three in number. These cells seem to take no part in the activities of the sac, and often disappear so quickly as to give rise to the impression, in

some cases, that no antipodals are formed. In fact, the claim of no antipodals should suggest the probability that the observer is dealing with the evanescent type. So far as researches have gone, this type is characteristic of the Amentiferæ and their allies, is found in Acer, etc.

2. Three large antipodal cells, increasing in size with the sac, sometimes extending almost half through its long diameter, apparently very active, and not disorganizing until after the embryo has begun to develop. This growth of the antipodals is usually associated with extensive division of the nuclei, mostly mitotic in our observations, but undoubtedly sometimes direct. This type is quite characteristic of the Ranunculaceæ and their allies.

3. Usually three comparatively permanent cells, not notable in size or activity, and usually associated with a sac decidedly narrowed at the antipodal end. This type is rather common among the Sympetalæ.

4. An indefinite number of cells, forming a relatively permanent and very prominent tissue, often continuing its growth downwards and breaking through the bottom of the sac. In this somewhat extensive growth the lowest cell is apt to become very large and vesicular, and multinucleate. This type is associated with a narrow, elongated sac, and is quite characteristic of certain sections of the Compositæ, notably the Asteroideæ.

## FERTILIZATION.

The phenomena of fertilization are the usual ones, but certain features seem worthy of mention. The pollen tube, after its entrance into the embryo sac, increases rapidly in diameter, in some cases forming a pouch-like tip remarkably large as compared with the caliber of the tube behind (*fig. 51*). The tube passes between one of the synergids and the wall of the sac, and the terminal pouch develops a convex and a concave side, so that the apex of the tube is directed towards the nucleus of the oosphere (*figs. 51, 52*). The tip of the tube apparently breaks down, as in all species we have investigated; at least it lacks

sharp definition and presents a frayed appearance. The distance between the two nuclei at the time of the discharge of the male cell is quite variable. In *fig. 52* it will be noted that the male cell has been discharged at some distance from the nucleus of the oosphere, and that the nourishing synergid gives no special indication of disorganization, unless it be found in the disappearance of the nucleolus. The nourishment of the male nucleus, however, during its movement towards the female nucleus, and increase in size, results in synergid disorganization. In *fig. 51* the two gamete nuclei are shown in a fusion stage, but it will be noted that the second male cell has also been discharged in a very disorganized condition. *Fig. 53* shows an undischarged pollen tube.

## ENDOSPERM.

The definitive nucleus is remarkably large, and rests either near the oosphere or becomes somewhat centrally placed in the sac (*figs. 46, 47, 52*). Free nuclear division, with more or less cytoplasmic organization, proceeds with great rapidity (*fig. 54*). In the figure just cited the oospore has not yet divided, while six free endosperm cells are represented. The prominence of the antipodal group is also noticeable, as well as its somewhat lateral position, due to the beginning of the remarkably one-sided development of the sac. That this formation of free endosperm cells proceeds not only with rapidity, but in a remarkably simultaneous fashion, is indicated by the great numbers of spindles in practically the same stage (*fig. 55*). The figure cited represents but a portion of the embryo sac. A more detailed view of an endosperm spindle is shown in *fig. 56*, in which the radiations about the poles are remarkably clear. During the formation of free endosperm cells the sac enlarges rapidly, both laterally and downward, but chiefly upon one side, so that eventually the still prominent and active antipodals are on one side of the lower broad end of the sac, and are frequently thrust out conspicuously into the cavity on a stalk-like projection, which represents the original center of the bottom of the sac (*fig. 57*). This is

decidedly different from the method of sac development in the monocotyls we have studied, in which the sac enlarges above the base, leaving the dwindling antipodals at the bottom of a pit-like depression, which sometimes is thrust to one side of the center. The one-sided development of the sac is determined by the fact that it is obstructed on one side by the conspicuous fibrovascular bundle, while the other side and bottom are directed towards the free cavity of the ovary.

At this stage of development the endosperm nuclei, formerly distributed through the cavity of the sac, have assumed the parietal position, forming a complete lining layer, interrupted only by the embryo and the antipodal stalk. It will be noted in the figure last cited that the embryo has completed only the first division.

The most interesting phenomenon in connection with the formation of endosperm, however, was the occasional evidence of its formation before the fusion of gametes, and even before the entrance of the pollen tube into the cavity of the sac. In *fig. 58* a preparation is shown in which the large egg is lying in the very apex of the sac, the two synergids being apparent in an adjacent section, and yet free endosperm nuclei are distributed through the sac, and are even assuming the parietal position.

It does not follow, however, that the endosperm begins to form without any stimulus from the pollen tube. The presence of the tube in the style is known to exert a strong influence upon the adjacent tissues, which may well be felt in the embryo sac. The beginning of endosperm formation, therefore, even though observed before the entrance of the pollen tube into the embryo sac, may none the less be definitely related to the phenomena of fertilization, of which the entrance of the tube and the fusion of the gametes are only a part.

The parietal placing of endosperm cells is a phenomenon of orientation which deserves consideration. That the curving of the tip of the pollen tube towards the nucleus of the oosphere and the movement of the male nucleus towards it are phenomena that depend upon chemotropism seems to be a satisfactory

explanation; but the parietal placing of free endosperm cells is not to be explained in any such way. The phenomenon may be likened to that observed in connection with certain animals and animal cells, which seek a solid support that seems to be essential to their further activity. In the case of endosperm cells the parietal position is usually antecedent to the formation of cell walls.

## EMBRYO.

There seems to be a general rule in the early divisions of the embryo, subject however to numerous exceptions, the causes of which are doubtless accessible. The oospore usually elongates considerably, with the nucleus at the distal extremity, and the vacuole conspicuous. The sequence of events in both *R. septentrionalis* and *R. multifidus* is so nearly identical that they will be considered together. As is to be expected, the first division is transverse, the terminal cell being smaller (often much smaller) than the other (*figs. 59–61*). In the last figure cited a sudden bending of the young embryo from the persistent synergid may be noted. The next division is also transverse, but it may occur either in the basal or apical cell (*figs. 62–65*). In the first figure cited the presence of a spindle in the basal cell definitely establishes the origin of the second wall in this case. There is also evidence that the second division may occur in the apical cell (*fig. 64*). In any event, a row of three cells seems invariable. Usually the third division is also transverse, apparently occurring in any one of the three cells previously formed, forming a row of four cells (*figs. 66–67*). This row of three or four cells uniformly precedes any longitudinal division. It would seem clear in this case that the suspensor may not arise wholly from the basal cell of the first division; and that the apical cell of the first division may contribute to the formation of the suspensor as well as to that of the embryo. After the row of three or four cells has been formed, the first longitudinal division occurs, and, so far as our preparations show, always in the apical cell (*figs. 68–70*). The persistence of the synergid unused in

the processes of fertilization is also evident. After the apical cell has divided longitudinally, similar divisions may occur in all other cells of the primary row or in some of them (*figs. 71–72*). This variation in the formation of longitudinal divisions in the suspensor region is apparent even in much older embryos. Occasionally a late transverse division in the basal cell was observed (*fig. 73*).

The most advanced stages of the embryo studied show considerable development of the suspensor, and the complete cutting off of a peripheral region of the embryo by periclinal walls, but no differentiation of the organs of the embryo.

The students who contributed preparations and drawings to this paper are O. W. Caldwell, T. C. Frye, Florence M. Lyon, W. D. Merrell, Mabel L. Merriman, J. H. Schaffner, and W. R. Smith. Their initials in connection with the drawings indicate the individual contributions. The laboratory work and the preparation of the plates were cared for by Dr. C. J. Chamberlain.

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## EXPLANATION OF PLATES IV–VII.

The drawings have been reduced to three-eighths of their original size, and were made with an Abbé camera. Unless otherwise indicated the ocular combination was Reichert ocular 4 and Bausch and Lomb $\frac{1}{12}$ oil immersion

### *PLATE IV.*

FIG. 1. Microsporangium of *R. septentrionalis*, showing row of hypodermal archesporial cells, in one of which is a spindle of the first periclinal division.

FIG. 2. Microsporangium of *R. multifidus*, in which the sporogenous cells are distinct, and the tapetal layer appears to have been developed from the wall. Leitz oc. 4, obj. *7a*.

FIG. 3. The same, with anther wall further developed. Same combination.

FIG. 4. Microsporangium of *R. septentrionalis*, in which the prominent tapetal layer seems to be more related to the sporogenous cells.

FIG. 5. Microsporangium of *R. multifidus*, showing a definite relation of tapetal cells to the wall layers, and a differentiation of the endothecium. Leitz oc. 4, obj. 7*a*.

FIG. 6. Microsporangium of *R. septentrionalis*.

FIGS. 7–11. Development of microspore tetrad in *R. septentrionalis*.

FIG. 12. Second nuclear division in pollen mother cell, occurring in same plane, and showing free nucleoli and kinoplasmic threads. Zeiss oc. 18, obj. $2^{mm}$.

FIG. 13. First nuclear division in pollen mother cell of *R. multifidus*, showing free nucleoli and polar radiations. Leitz oc. 4, obj. $\frac{1}{12}$.

FIG. 14. First nuclear division in pollen mother cell of *R. multifidus*, showing "centrospheres."

FIG. 15. Microspores of *R. septentrionalis*, showing thin areas in the exospore. Leitz oc. 4, obj. 7*a*.

FIGS. 16, 17. Mature microspores of *R. septentrionalis*, showing the two nuclei.

FIGS. 18–20. Macrosporangium of *R. septentrionalis*, with single archesporial cell; in *fig. 20* a periclinal division is represented in the overlying epidermal cell.

FIG. 21. The same, showing subjacent row of cells in the sporangium sometimes mistaken for a row of mother cells.

FIG. 22. The same, showing enlargement and first nuclear division.

FIG. 23. The same, showing the first division completed.

FIGS. 24, 25. Archesporium of *R. septentrionalis*, composed of more than one cell.

*PLATE V.*

FIG. 26. Macrosporangium of *R. septentrionalis*, with eight-celled archesporium.

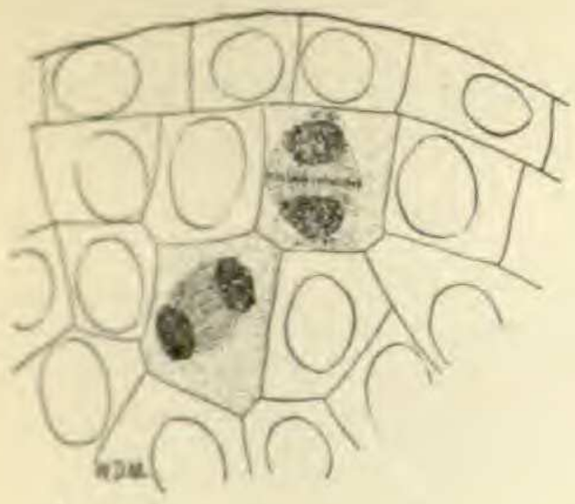
FIG. 27. The same, with three archesporial cells in an advanced stage of development, the two to the right in the "two-celled" and "four-celled" stages of the embryo sac. Zeiss oc. 4, obj. $2^{mm}$.

FIG. 28. Macrosporangium of *R. multifidus*, with the remains of a second archesporial cell.

FIGS. 29–31. The same, showing successive stages in the development of the row of four mother cells.

FIG. 32. The same, showing the beginning of the enlargement of the fertile mother cell, and the destruction of the adjacent cell.

FIG. 33. Macrosporangium of *R. abortivus*, showing a two-celled archesporium.



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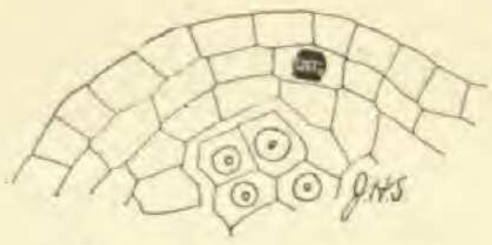

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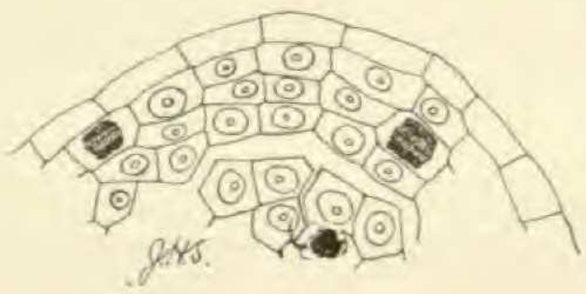

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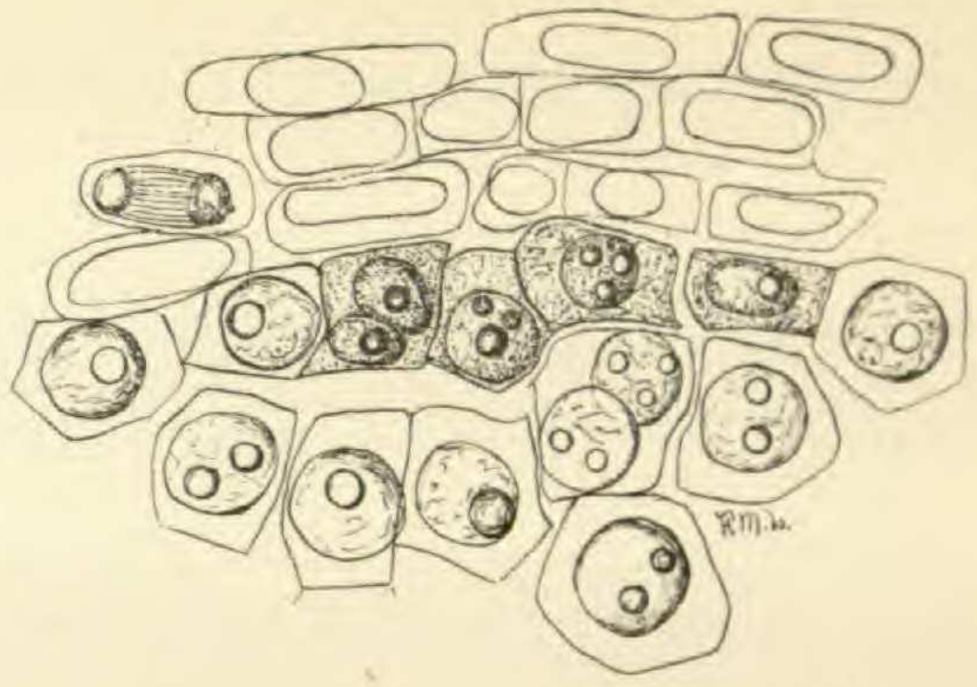

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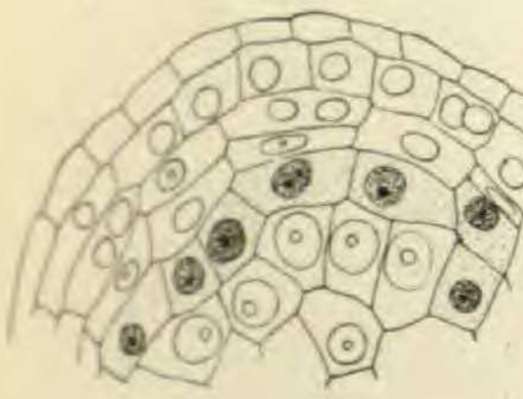

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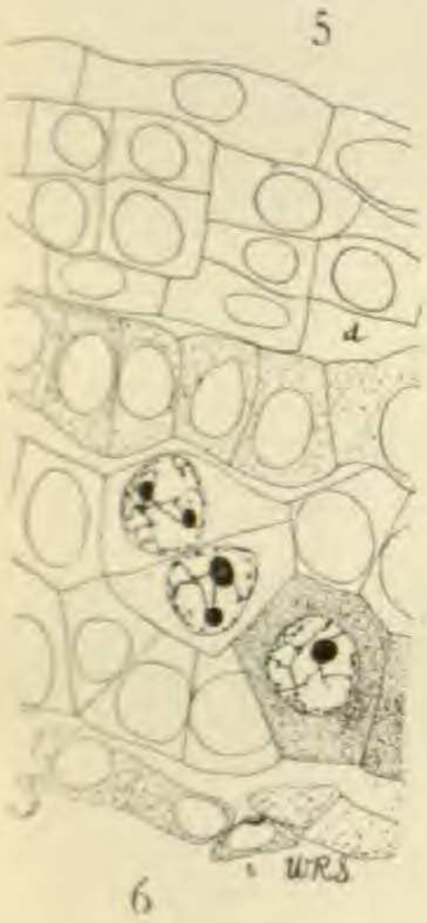

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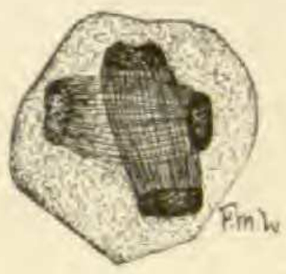

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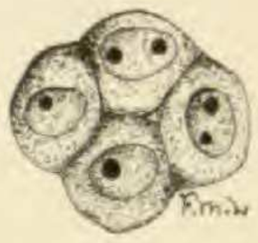

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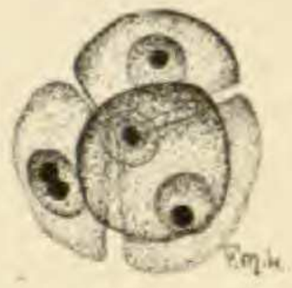

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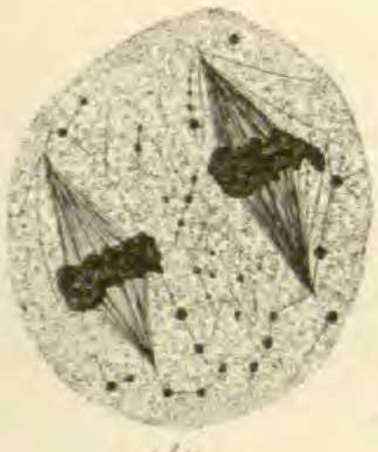

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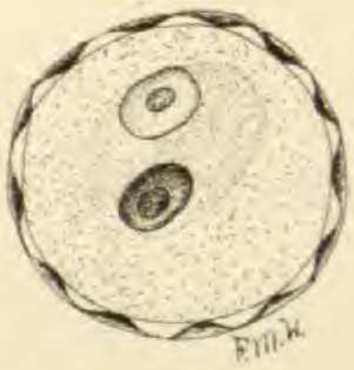

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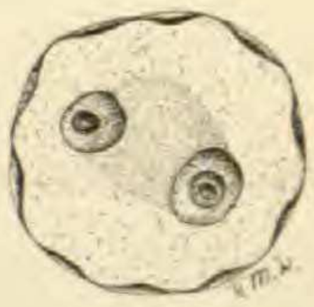

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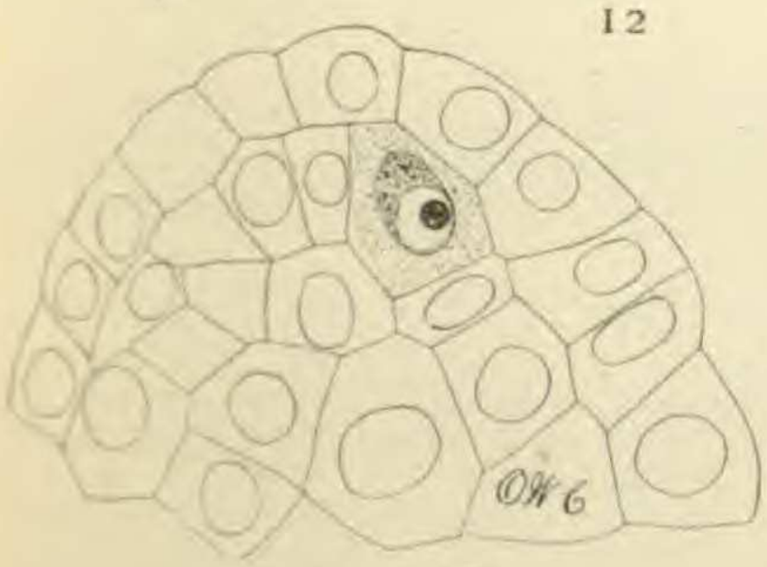

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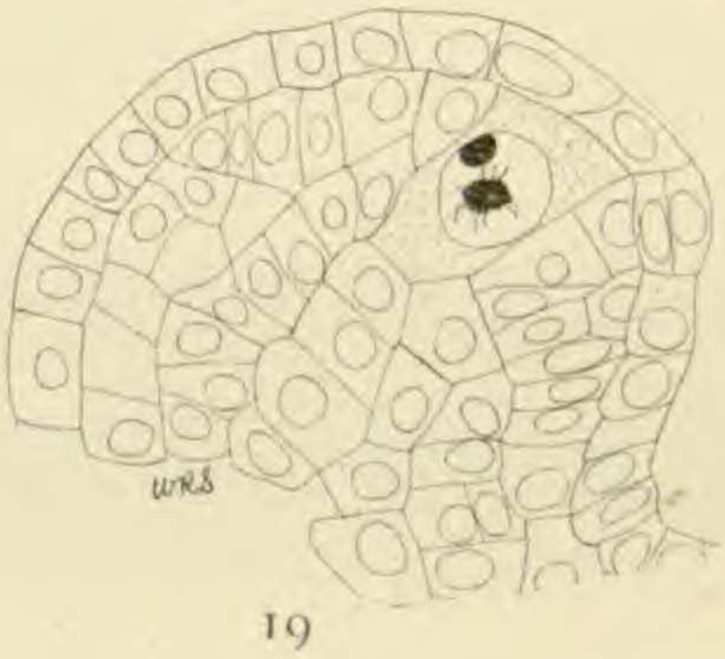

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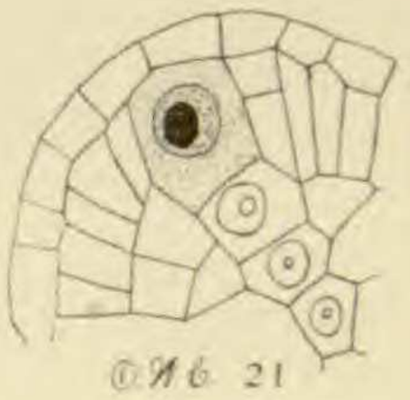

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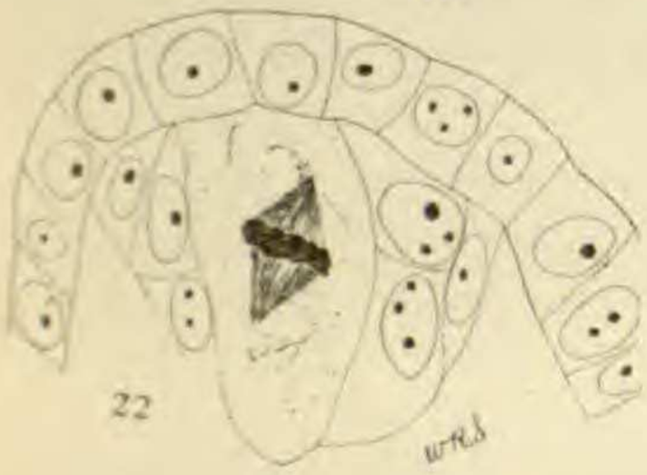

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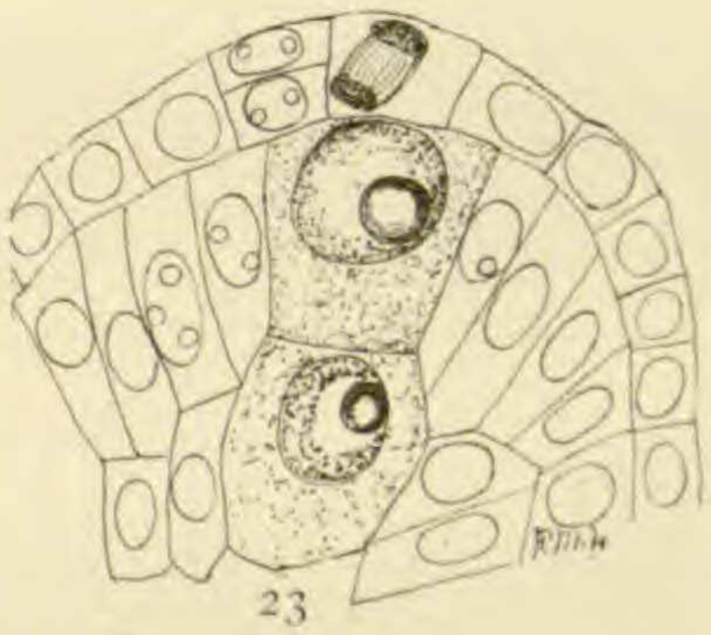

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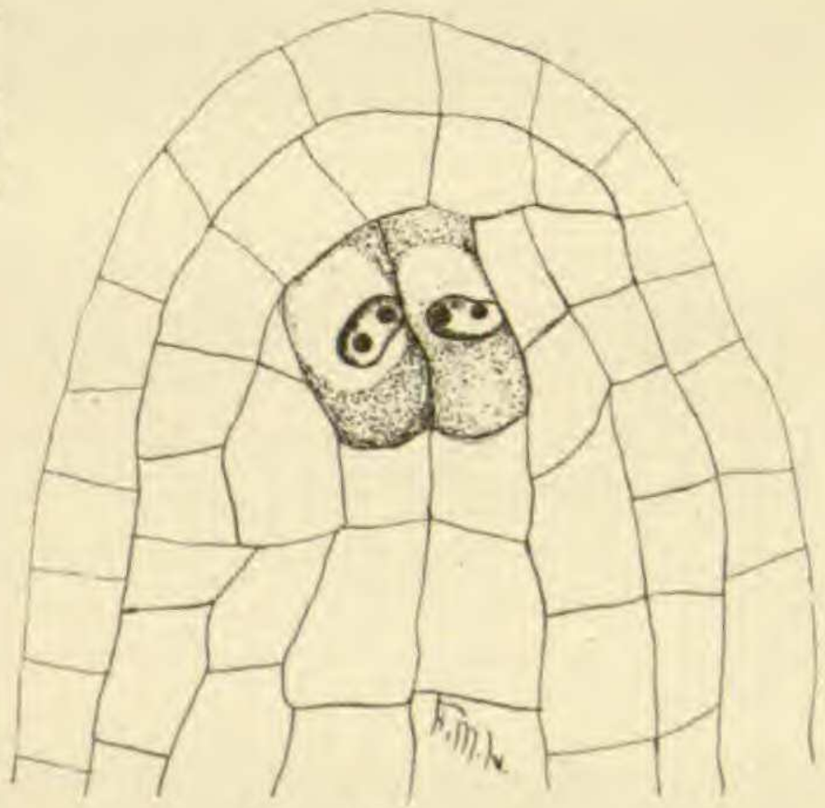

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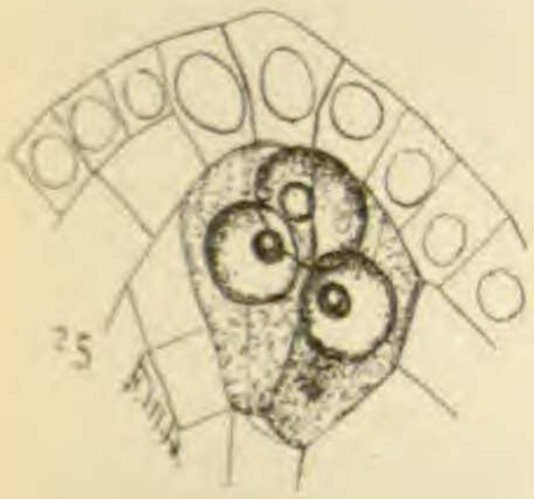

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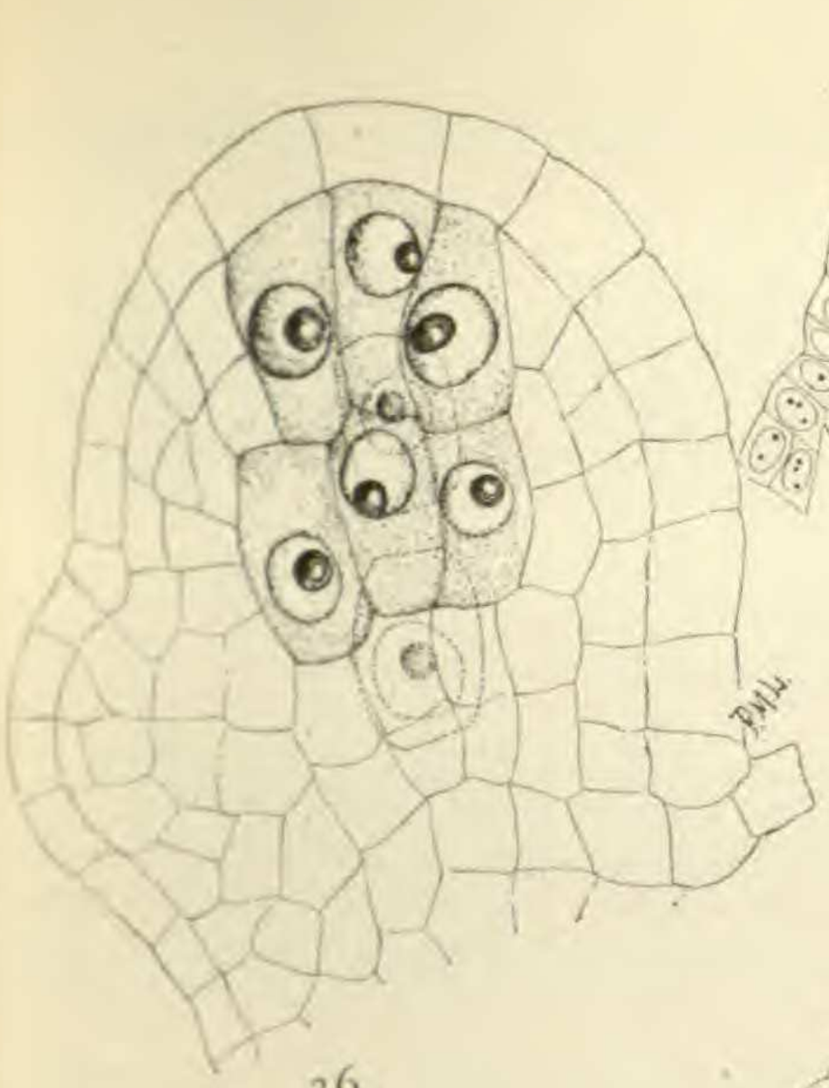


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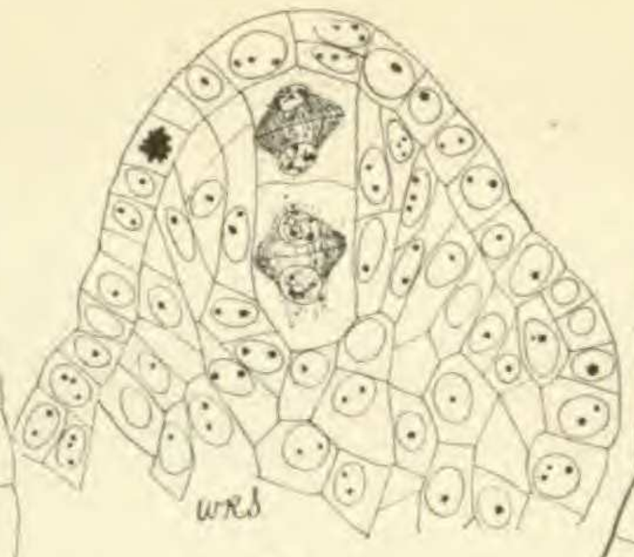


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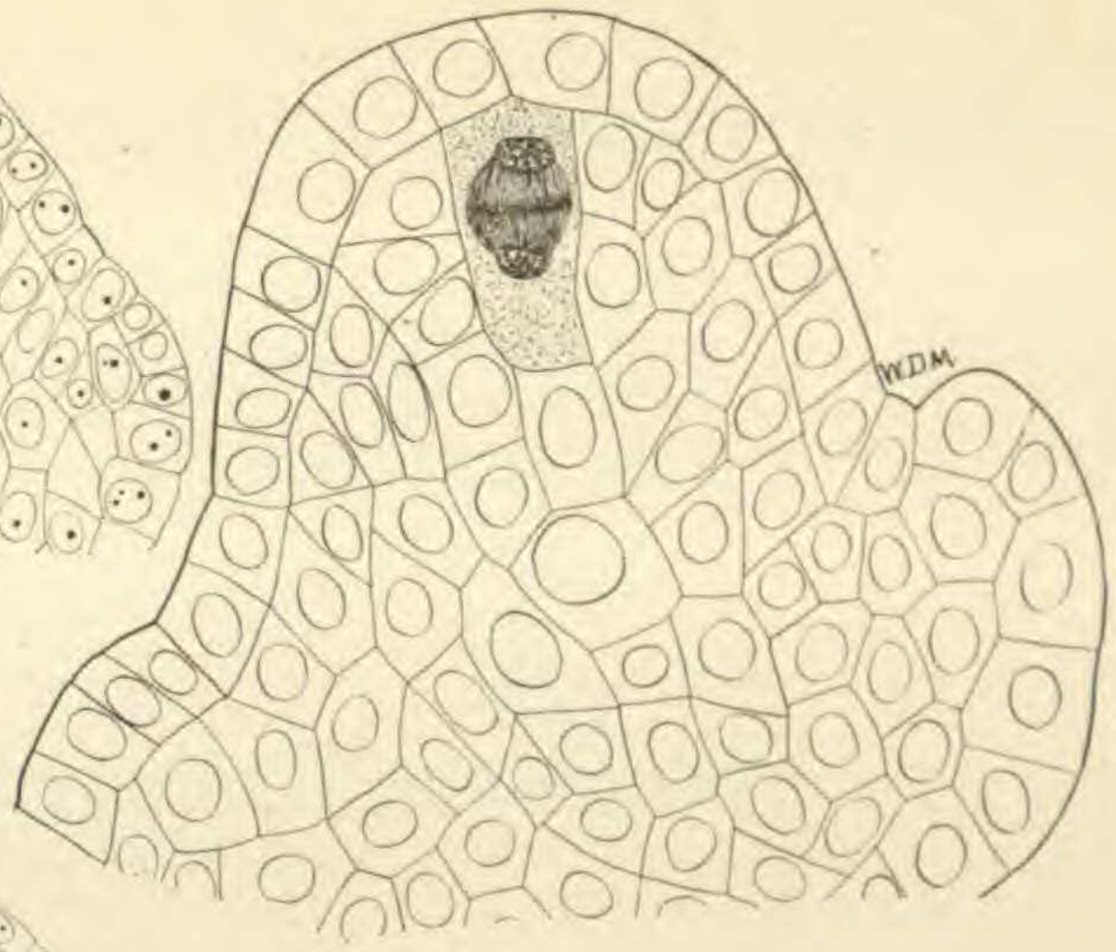


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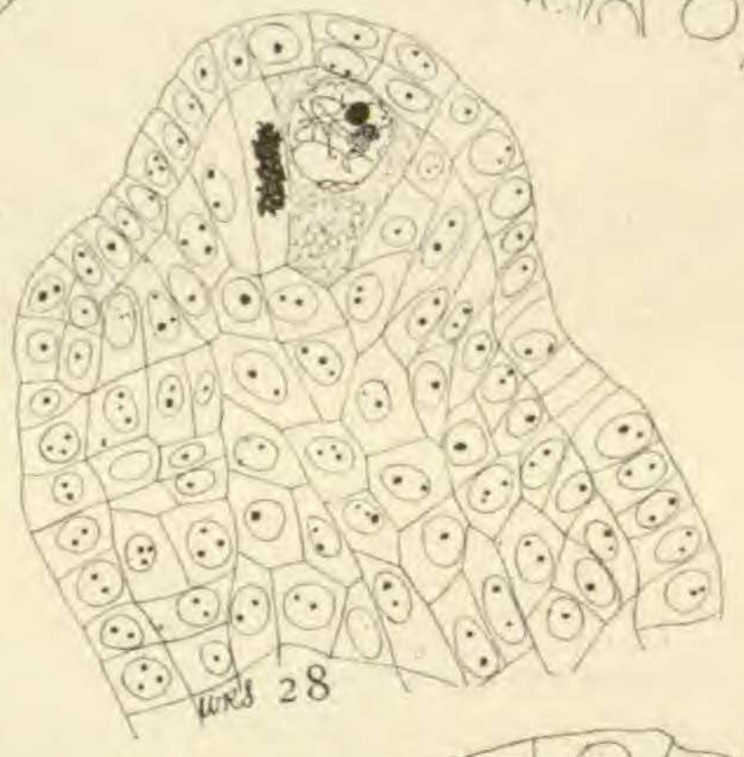


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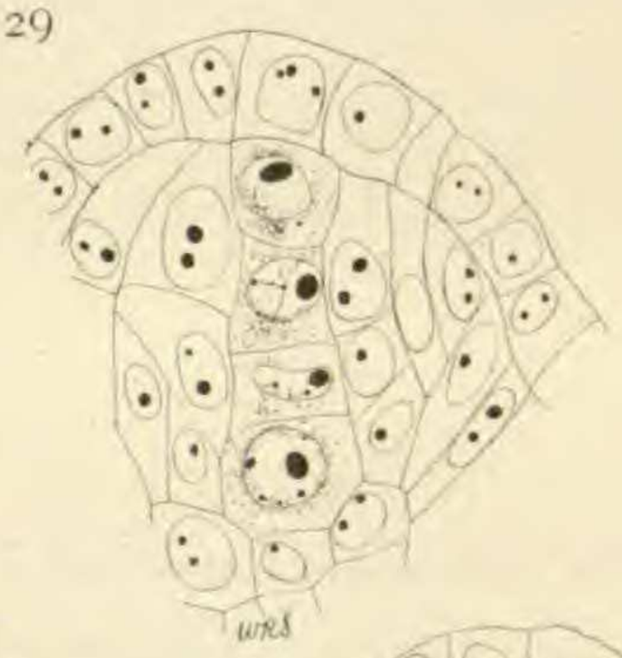


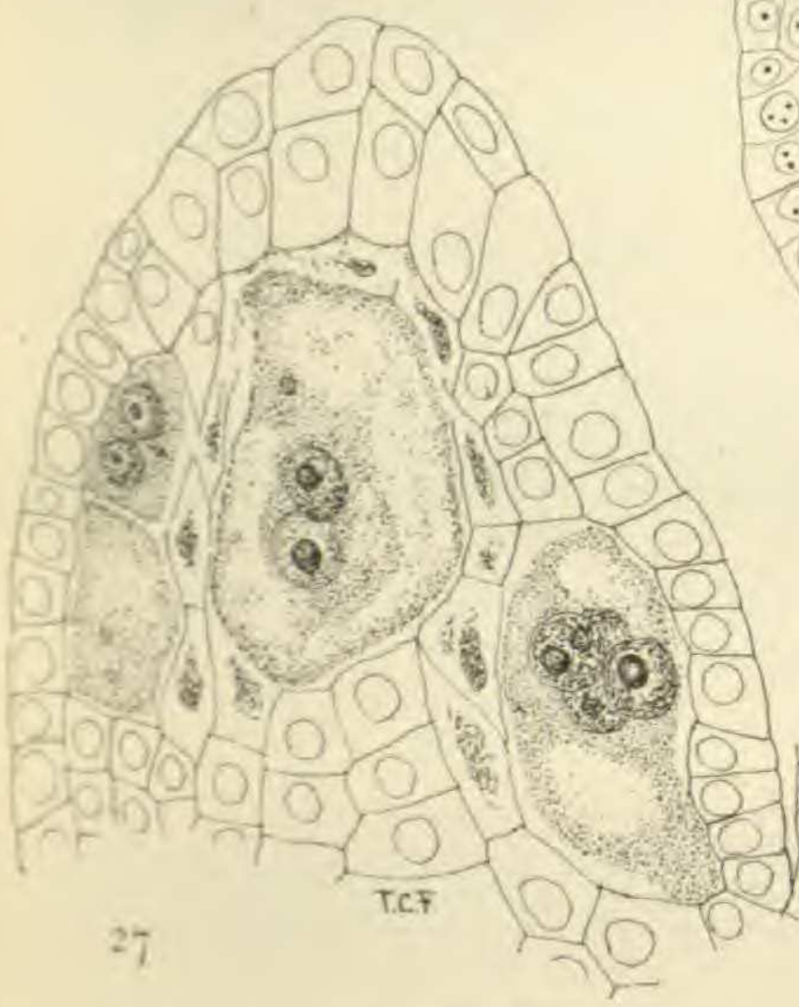


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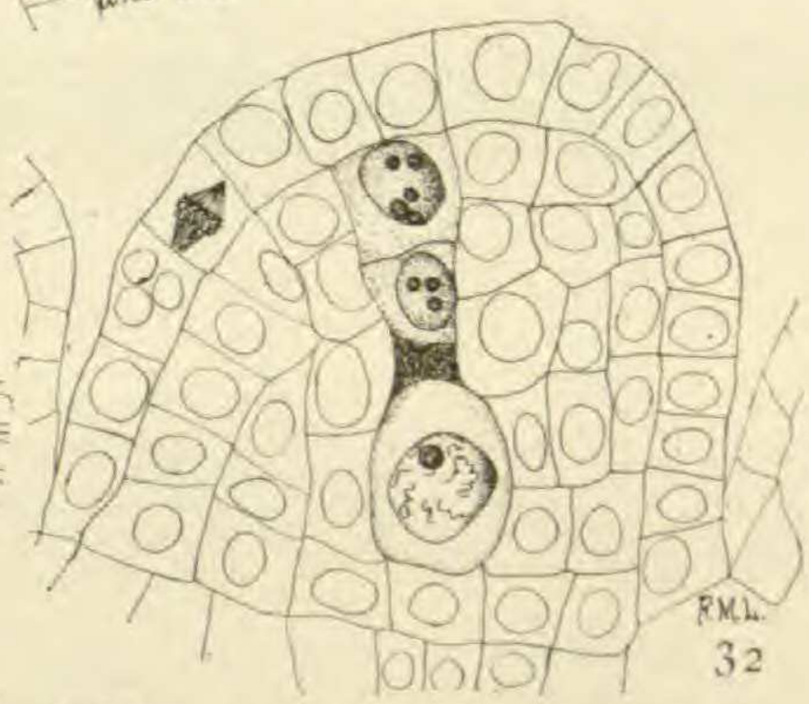


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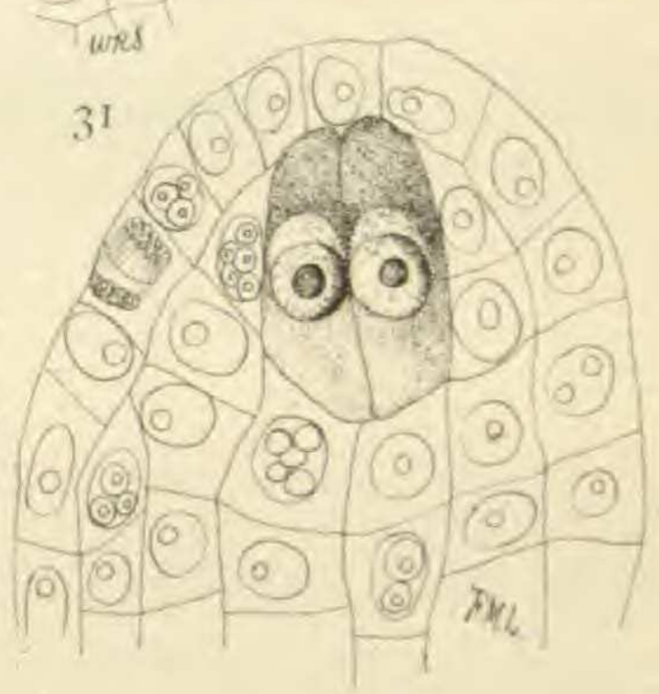


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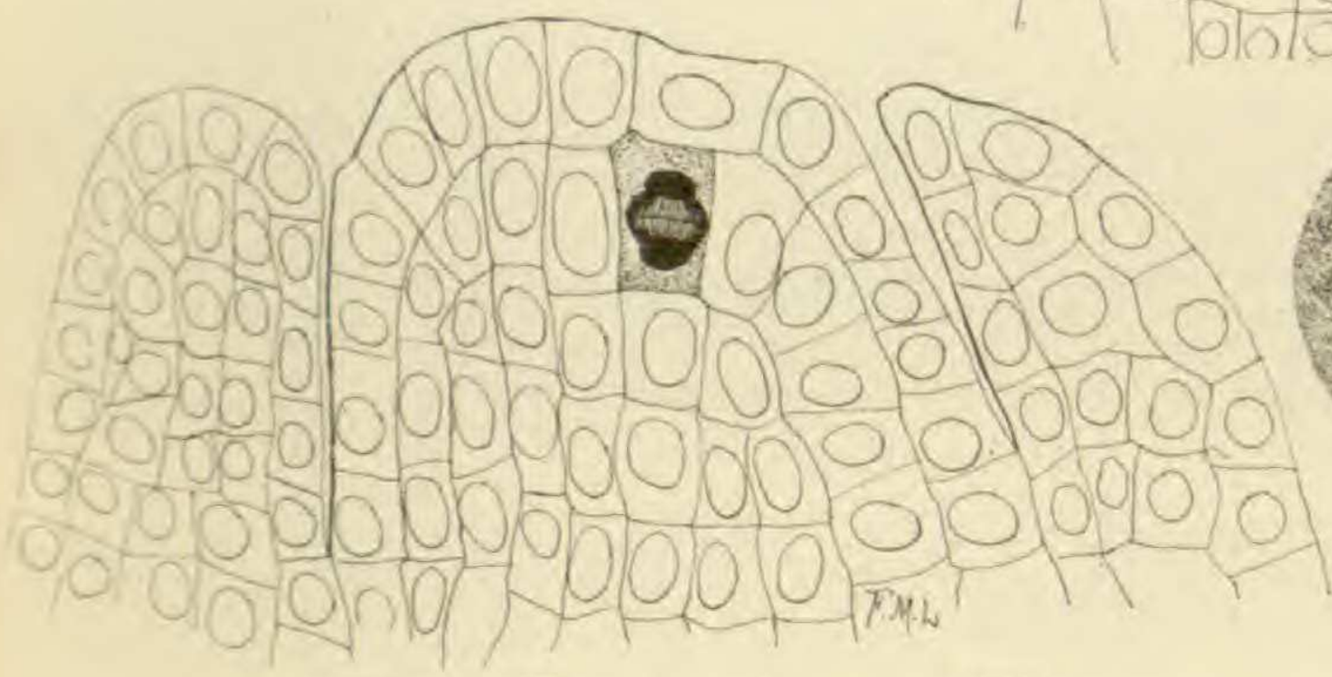


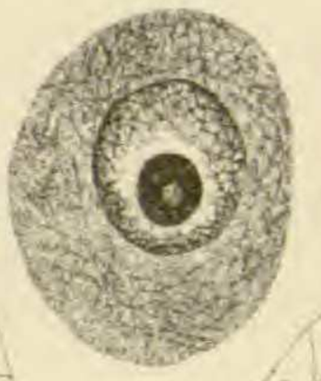

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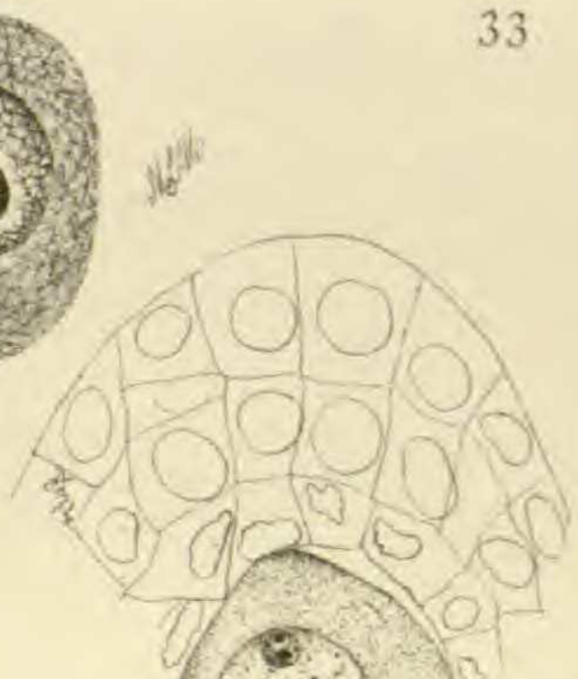

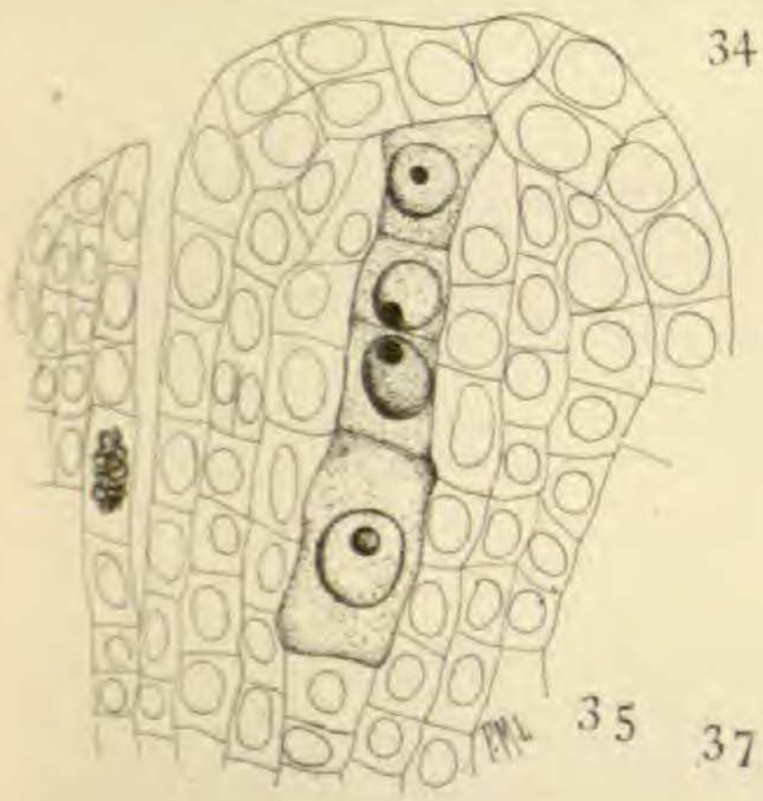


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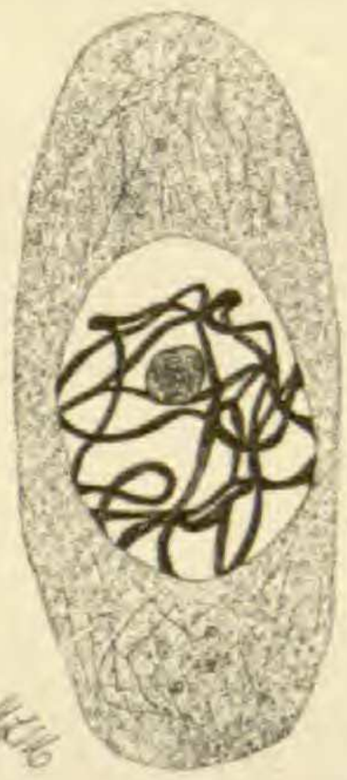

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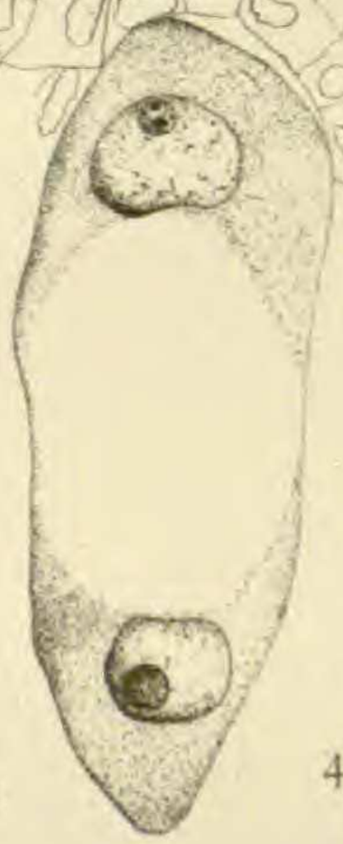

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